Canopy-level photosynthetic compensation after defoliation in a tropical understorey palm

Anten N. P. R., Ackerly D. D.
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Abstract

1. Increases in photosynthesis of leaves remaining after defoliation may result from shifts in leaf photosynthetic characteristics or from an improved light penetration in the canopy. However, few studies have tried to estimate the relative contribution of these factors to mitigating the negative effects of defoliation. We present a quantitative framework for such an analysis.

2. In a field and greenhouse experiment, plants of the rain forest understorey palm *Chamaedorea elegans* were subjected to three levels of defoliation (0, 50 or 66% of leaves removed) and, in the greenhouse, grown at two irradiances (5 or 16% of daylight, 'low light' and 'high light' hereafter). For each plant, leaf photosynthesis and light penetration in the canopy were measured and these data were used to calculate whole-canopy carbon gain.

3. Defoliation significantly increased the light available to the remaining leaves. In the field and in the 'high-light' greenhouse plants, defoliation also resulted in an increase in the light-saturated photosynthesis per unit leaf area (P_{max}), although in the 'low-light' plants this was not the case.

4. A sensitivity analysis revealed that in the 'low-light' plants, a proportional increase in leaf P_{max} did not result in increased canopy-level carbon gain, while in the 'high-light' and field plants, it did. This suggests that the lack of plasticity in P_{max} in response to defoliation, at low light, may be the appropriate pattern to maximize carbon gain.

5. Defoliated plants had 10–18% more average photosynthesis per unit leaf area (P_{area}) than the control plants, and this increase was mostly the result of an improved light penetration in the canopy.

6. A relatively small fraction (5–30%) of the total estimated loss in canopy carbon gain caused by the removal of leaves was compensated for by an increase in P_{area}. This

suggests that in rain forest understorey plants, an increase in diurnal photosynthesis of remaining leaves has limited potential for mitigating the negative effects of defoliation.

Introduction

Plants in the understorey of tropical rainforests are often subjected to physical damage from falling canopy debris (**Clark & Clark 1989**; **Chazdon 1991**) or herbivory (**Dirzo 1984**; **Marquis 1984**), both of which may result in considerable loss of leaf area. Given the poor light availability in the understorey of a tropical rain forest (**Chazdon 1986**) and the importance of light for photosynthesis and growth, these plants might be restricted in their ability to recover from defoliation. However, various studies have shown that rain forest understorey plants are able to continue or even increase growth after partial or complete defoliation (**Mendoza *et al.* 1987**; **Oyama & Mendoza 1990**; **Chazdon 1991**).

Shifts in leaf physiological characteristics in partially defoliated plants may mitigate the negative impacts of defoliation (**McNaughton 1979**; **Nowak & Caldwell 1984**). Indeed, increases in the light-saturated rate of photosynthesis (P_{max}) of leaves after partial defoliation have been observed in many species (e.g. **Nowak & Caldwell 1984**; **von Caemmerer & Farquhar 1984**; **Senock *et al.* 1991**; **Ovaska *et al.* 1992**). However, this phenomenon has not been studied in forest understorey plants. Increases in P_{max} after defoliation have been associated with an improved availability of water, nutrients and root-produced cytokinins to the remaining leaves (**Wareing *et al.* 1968**) and with a reduced accumulation of assimilates in the leaves due to an improved source–sink ratio (**Neales & Incoll 1968**).

Apart from its effect on leaf photosynthetic traits, defoliation may also increase the photosynthesis of remaining leaves because it can facilitate increased light penetration if the removed leaves were previously shading others. For grasses, several studies (**Gold & Caldwell 1990**; **Senock *et al.* 1991**) found that removing 50% or more of the leaf area of plants resulted in a considerable increase in the amount of direct radiation received by the remaining leaves. However, in understorey plants, which tend to have canopies with minimal self-shading (**King 1991**; **Chazdon 1985**; **Kohyama 1991**), the effects of defoliation on light penetration through the canopy are probably not as strong as in herbaceous plants, which tend to form dense canopies with strong vertical light gradients (**Monsi *et al.* 1973**).

To understand the ecological significance of shifts in leaf photosynthetic traits and canopy structure in response to defoliation, it is important to quantify the effects of these changes on whole-plant carbon gain. Differences in leaf photosynthetic capacity often have relatively little effect on whole-plant carbon gain compared to differences in canopy structure (e.g. **Monsi *et al.* 1973**; **Barnes *et al.* 1990**), particularly at low light (**Sims *et al.* 1994**; **Hikosaka *et al.* 1999**). This is because there is generally a strong positive correlation between a leaf's photosynthetic capacity and its rate of dark respiration (**Hirose & Werger 1987**; **Pons *et al.* 1989**; **Anten *et al.* 1995, 1996**), and dark respiration is a particularly important component of whole-plant carbon gain at low light (**Hirose & Werger 1987**; **Sims *et al.* 1994**). Interestingly, **Gold & Caldwell (1990)** found an increase in photosynthesis per unit leaf area of remaining leaves of the grass *Agropyron desertorum* after defoliation and found this increase to be more strongly correlated with an improved light availability than with changes in leaf photosynthetic traits. However, no studies have analysed the relative importance of

changes in leaf photosynthetic characteristics *vs* reduced self-shading for whole-plant carbon gain following defoliation.

Here, we develop a simple model for quantifying the effects of shifts in leaf photosynthesis and canopy structure on whole-canopy carbon gain and estimating photosynthetic compensation at the whole-plant level. This model was applied to a field and greenhouse experiment with the neotropical understorey palm *Chamaedorea elegans*, in which plants were subjected to different levels of defoliation and, in the greenhouse, grown at different irradiances. Palms are very common in the understorey of tropical rain forests. Their simple monopodial growth form, with leaves being produced along a single stem, makes them ideally suited to analyse effects of defoliation on canopy structure and whole-plant carbon gain. In addition, leaves of many palm species including *C. elegans* are collected by local people and used for a variety of purposes, and it is therefore important to investigate the impact of leaf harvesting on the performance of individual palm plants (**Oyama & Mendoza 1990**). From each plant, leaf harvesters typically remove up to 50% of the newly produced leaves (**Reining *et al.* 1992**; Miguel Martinez-Ramos, personal communication).

The objectives of this study were: (i) to investigate the effect of partial defoliation on the photosynthetic characteristics of remaining leaves and on the light distribution in the canopy; and (ii) to quantify the relative contributions of these changes in leaf photosynthesis and canopy structure to whole-plant carbon gain and the extent to which these changes mitigate the losses imposed by defoliation.

Model